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Risk avoidance in sympatric large carnivores: reactive or predictive?

Femke Broekhuis[1,2], Gabriele Cozzi[2,3], Marion Valeix[1,4], John Weldon McNutt[2], David W. Macdonald[1]

[1] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney, OX13 5QL, UK

[2] Botswana Predator Conservation Trust, Maun, Botswana

[3] Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

[4] Laboratoire de Biométrie et Biologie Evolutive, Centre National de la Recherche Scientifique (CNRS) - Unité Mixte de Recherche (UMR) 5558, Université Claude Bernard–Lyon 1, Bâtiment Gregor Mendel, 43 boulevard du 11 novembre 1918, 69622 Villeurbanne cedex, France

Corresponding author: Femke Broekhuis

Email: femke.broekhuis@zoo.ox.ac.uk

Phone: +44 1865 611 106

Fax: +44 1865 611 101

Running title: Risk avoidance - reactive or predictive?

Abstract

1. Risks of predation or interference competition are major factors shaping the distribution of species. An animal's response to risk can either be reactive, to an immediate risk, or predictive, based on preceding risk or past experiences. The manner in which animals respond to risk is key in understanding avoidance, and hence coexistence, between interacting species.
2. We investigated whether cheetahs (*Acinonyx jubatus*), known to be affected by predation and competition by lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*), respond reactively or predictively to the risks posed by these larger carnivores.
3. We used simultaneous spatial data from Global Positioning System (GPS) radio-collars deployed on all known social groups of cheetahs, lions and spotted hyaenas within a 2700 km^2 study area on the periphery of the Okavango Delta in northern Botswana. The response to risk of encountering lions and spotted hyaenas was explored on three levels: short-term or immediate risk, calculated as the distance to the nearest (contemporaneous) lion or spotted hyaena, long-term risk, calculated as the likelihood of encountering lions and spotted hyaenas based on their cumulative distributions over a six month period and habitat associated risk, quantified by the habitat used by each of the three species.
4. We showed that space and habitat use by cheetahs was similar to that of lions and, to a lesser extent, spotted hyaenas. However, cheetahs avoided immediate risks by positioning themselves further from lions and spotted hyaenas than predicted by a random distribution.
5. Our results suggest that cheetah spatial distribution is a hierarchical process, firstly driven by resource acquisition and thereafter fine-tuned by predator avoidance; thus suggesting a reactive, rather than a predictive, response to risk.

Key-words: African carnivores, avoidance behaviour, ecology of fear, intraguild coexistence, landscape of risk

Introduction

The risk of predation or interference competition can significantly alter animal behaviour and species' spatial distribution (Ripple & Beschta 2004; Fortin *et al.* 2005; Berger & Gese 2007). However, the probability of costly encounters can be minimised as risk is not homogenously distributed in space and time, but rather varies with the distribution, density, habitat use and activity of predators and competitors (Brown, Laundre & Gurung 1999). This heterogeneity allows animals to use 'refuges', i.e. areas of low risk (Durant 1998; Chesson 2000) or adjust their behaviour, for example habitat use or anti-predator behaviours such as vigilance, in response to changing levels of risk (Laundré, Hernández & Altendorf 2001; Creel *et al.* 2005).

Such a response to risk can either be reactive or predictive. A reactive response to risk is based on an animals' knowledge of actual, real-time risk. Elk (*Cervus elaphus*, Linnaeus), for example, used coniferous woodland, rather than grassland, when wolves (*Canis lupus*, Linnaeus) were in the immediate vicinity (Creel et al. 2005). Similarly, African buffalo (*Syncerus caffer*, Sparrman) visited waterholes during the hot, midday hours, rather than at dawn and dusk, when lions (*Panthera leo*, Linnaeus) were nearby (Valeix *et al.* 2009a). A predictive response, on the other hand, is based on a pre-emptive response to a potential for risk, derived from previous knowledge of the competitors or predators' whereabouts or the habitat types intensively used by them. For instance, browsers such as kudu (*Tragelaphus strepsiceros*, Pallas), giraffe (*Giraffa camelopardalis*, Linnaeus) and impala (*Aepyceros melampus*, Lichtenstein) were less likely to select areas where there was a long-term risk of predation by lions (Valeix *et al.* 2009b). These behavioural responses to risk are, however, by no means limited to predator-prey interactions and numerous studies have observed similar responses between predators and humans (e.g. Woodroffe 2011; Valeix *et al.* 2012) and between competing carnivores (e.g. Creel, Spong & Creel 2001; Berger & Gese 2007). Whilst several studies have investigated reactive and predictive avoidance between carnivores independently (e.g. Durant 1998; Durant 2000) these two types of avoidance in African carnivores have not yet been investigated simultaneously using the same set of data. Here we investigate

72 the reactive and predictive response of cheetahs (*Acinonyx jubatus*, Schreber) to the actual (i.e. short-
73 term) and the prospective (i.e. long-term) risk of encountering lions and spotted hyaenas (*Crocuta*
74 *crocuta*, Erxleben).
75
76 Due to their smaller body size and solitary nature, cheetahs are competitively subordinate to the larger
77 and more social lions and spotted hyaenas (Caro 1994; Durant 1998; Durant 2000). These larger predators
78 present real threats to cheetahs: in the Serengeti National Park, Tanzania, for example, lions and spotted
79 hyaenas were reported to be responsible for 73% of cheetah cub mortality and the kleptoparasitism of
80 12.9% of cheetah kills (Laurenson 1995; Hunter, Durant & Caro 2007b). Hence, cheetahs have been
81 described as a 'refugial species', and spatial avoidance is believed to be one of the main mechanisms by
82 which these competitively subordinate carnivores can minimise interactions with more dominant ones
83 (e.g. Durant 1998).
84
85 To determine whether spatial avoidance of larger carnivores by cheetahs is reactive or predictive, we
86 investigated both the effects of the short-term risk of encountering lions and spotted hyaenas (assessed
87 by the distance to the nearest lion and spotted hyaena) and the long-term risk of encountering these
88 predators (based on habitat use and a landscape of risk representing the likelihood of lion and spotted
89 hyaena presence calculated over six months) on the spatial distribution of cheetahs.

90 More specifically we expected that:

91 1. Cheetahs avoided areas that are intensively used by lions and spotted hyaenas (long-term risk),
92 2. Cheetahs avoided immediate, short-term encounters with lions and spotted hyaenas (short-term
93 risk),
94 3. Cheetah habitat use was negatively influenced by the habitat used by lions and spotted hyaenas,
95 4. The response to short- and long-term risks changed depending on the structural characteristics of
96 the habitat.

To test these predictions we used simultaneous GPS (Global Positioning System) radio-collar data from cheetahs, lions and spotted hyaenas in northern Botswana.

Methods

Study area

This research took place on the periphery of the Okavango Delta, a permanent inland delta situated in northern Botswana. The study site (centred at 19°31'S, 23°37'E; elevation ca. 950m) encompassed an area of approximately 2 700 km^2 and included the south-eastern part of Moremi Game Reserve and the adjacent Wildlife Management Areas (for details see McNutt 1996; McNutt & Silk 2007). The area lies in a semi-arid ecosystem characterised by five distinct habitat types (Table 1 and see below). The climate is characterised by two distinct seasons; a dry season between April and October and a wet season between November and March with an annual rainfall of 450-600 mm (Mendelson, Vanderpost & Ramberg 2010).

Using a digitalised vegetation map with an accuracy of 74 – 77 % (see Ringrose *et al.* 2005 for more details) a map with the five different habitat types was created by merging habitat types with a similar vegetation composition and structure (Table 1). Within each of these habitat types the visibility, and hence we assume detectability, was constant across season (Cozzi 2012, page 101). The area has a sedentary prey base characterised by a variety of herbivore species ranging from the small ungulates including steenbok (*Raphicerus campestris,* Thunberg), warthog (*Phacochoerus africanus*, Pallas) and impala to the larger species such as African buffalo, giraffe, African elephant (*Loxodonta Africana*, Blumenbach). The prey abundance did not fluctuate with season (Bartlam 2010).

Data collection

Carnivore data - Between October 2008 and July 2011 we fitted GPS radio-collars (VECTRONIC Aerospace GmbH, Germany) on six adult cheetahs, five adult lions in distinct neighbouring social groups and eight

121 adult spotted hyaenas in five different neighbouring social groups. The radio-collars were deployed on all
122 known social groups within the study area and the three species overlapped extensively in space. The
123 radio-collars were programmed to collect GPS fixes four times a day for cheetahs (00h00, 06h00, 12h00
124 and 18h00) and eight times a day for lions and spotted hyaenas (00h00, 02h00, 04h00, 06h00, 12h00,
125 18h00, 20h00 and 22h00). For accuracy, GPS fixes with a dilution of precision (DOP) > 10 were removed
126 (Frair et al. 2010).
127
128 *Analyses*

129 For all three species we first assessed their general habitat selection. We then investigated whether the
130 probability of cheetah presence was influenced by the long-term risk of encountering lions or spotted
131 hyaenas and/or their immediate proximity and explored whether these relationships were influenced by
132 the habitat. All data extractions and calculations were carried out either in Geospatial Modelling
133 Environment (GME) (Beyer 2012; R Development Core Team 2012) or ArcGIS 10.0 (Environmental
134 Systems Research Institute Inc. 2010).

135 Due to the timing of when radio-collars were deployed, we used three different datasets. We used data
136 on cheetahs, lions and spotted hyaenas collected between October 2008 and July 2011 to determine
137 species-specific habitat selection. We then used two different datasets, each of six months, to investigate
138 cheetah response to short- and long-term risk; 1) when cheetahs and lions were collared simultaneously
139 (September 2010 - March 2011) and 2) when cheetahs and spotted hyaenas were collared simultaneously
140 (August 2009 - February 2010). During both these periods none of the female cheetahs had dependent
141 cubs. The subsequent analyses on short- and long-term risk are the same for both these datasets.

142

143 *Habitat selection*

144 To test whether cheetahs, lions and spotted hyaenas selected for specific habitat types we carried out a
145 compositional analysis (Aebischer, Robertson & Kenward 1993) using the package 'adehabitatHS' in the
146 statistical software R (Calenge 2006; R Development Core Team 2012). During the period between
147 October 2008 and July 2011 several of the female cheetahs had cubs but all were lost within the first
148 month. However, to minimise the influence of temporary site fidelity i.e. denning, we randomly selected
149 1000 GPS points per individual. We then analysed the data on two scales. First, the proportion of habitat
150 types within the home-range of each individual was compared to the proportion of habitat types
151 available within the study area (Johnson 1980; 2nd order habitat selection). Second, habitat types at each
152 GPS location were compared to habitat types available within the home-range of the respective individual
153 (Johnson 1980; 3rd order habitat selection). Home-ranges were based on the 90% isopleth (Börger et al.
154 2006) from kernels created using fixed Gaussian Kernel Density Estimate (KDE) function. Kernel
155 bandwidth was estimated using the Least Square Cross Validation (LSCV) method (Powell 2000; Gitzen,
156 Millspaugh & Kernohan 2006). The study area was defined by the outermost boundary delimiting the
157 total sum of the 90% kernels of all three species (n=19). The Ivlev's electivity index was used to
158 investigate whether each species used habitat types in accordance to their availability (Krebs 1999). The
159 formula $E=(p-q)/p+q)$ standardised the habitat used (p) to the habitat available (q) with values ranging
160 from -1 to 1. Habitat preference occurred when p was greater than q ($E>0$) and avoidance when p was
161 less than q ($E<0$) (Krebs 1999). Ivlev indices were calculated for both the 2nd order (home-ranges vs. study
162 area) and 3rd order (locations vs. home-ranges) habitat selection.

163

164 *Long- and short-term risk of encountering larger carnivores*

165 We built 'landscapes of risk' derived from the ranging data of lions and spotted hyaenas over six months
166 to reflect the probability of their presence over the long-term. These landscapes were based on kernel
167 density estimates (see above), and each individual kernel density estimate was rasterized (cell size: 50 x
168 50 m) so the value of each pixel of the raster map was a proxy of the likelihood of encountering a

169 predator. Once all the individual maps were created they were summed per species to create a species-
170 specific landscape of risk. Short-term risk was assessed by calculating the distance to the nearest lion and
171 spotted hyaena.

172 Whilst uncollared individuals could not be accounted for we believe this problem to be minimal,
173 especially for lions. Based on a full count of the adult lion population during the six month period of
174 overlapping lion and cheetah data, we estimated that 35 % of the lion population was collared.
175 Furthermore, pride females were seen together 78.6 ± 6.6 % (mean ± 95 % CI) of the time (F. Broekhuis,
176 unpublished data) suggesting that the collared animals are representative of the spatial behaviour of the
177 group they belong to. In addition, we only used cheetah data that fell within the 90% lion kernels, thereby
178 minimising the edge effects where unknown lions could overlap with the collared cheetahs. Accounting
179 for uncollared spotted hyaenas was more difficult. Based on a spotted hyaena density of 15.4 individuals
180 per 100km^2 (G. Cozzi pers. comm.) we estimated that approximately 2 % of the spotted hyaena
181 population in the study area was collared. Whilst this a comparatively small number of the total
182 population we believe that this should not limit the long-term risk analysis as individuals within a clan
183 overlap extensively (Boydston *et al.* 2003). However, because of the strict linear hierarchical social
184 organisation of spotted hyaenas clans, individuals might exhibited fine-scale differences in habitat use
185 (Kruuk 1972) which we accounted for by deploying several collars within each clan. Analysing the
186 response to the distance to the nearest spotted hyaena is possibly less informative as clan members often
187 split into smaller sub-groups and are rarely, if ever, all found together.
188

189 *Statistical analyses*

190 The effect of both long- and short-term risk of encountering larger carnivores on the probability of
191 cheetah presence was analysed using generalized linear mixed models (GLMM) with a binomial error
192 structure and logit-link function. The binomial response variables were 0/1 – where 1 represented the
193 GPS locations for cheetah and 0 the randomly generated points. To test whether the probability of finding

194 a cheetah was influenced by the long-term risk of encountering lions and spotted hyaenas, we compared
195 the 'landscape of risk' value at actual GPS locations of each cheetah to the risk at randomly generated
196 points (Manly et al. 2002). We randomly selected 500 GPS locations per cheetah and generated the same
197 number of random points within each species-specific landscape of risk. To test whether cheetahs were
198 closer (or further away) from predators than expected assuming a random distribution, we compared the
199 distance from each cheetah GPS location to the nearest lion and spotted hyaena to the distance that
200 these predators were to randomly generated points. We randomly selected 500 GPS locations per
201 cheetah and selected the same number of random points within the cheetah's home-range. Each random
202 point was associated with the same time sequence that mimicked that of the cheetah.

203 For the long-term risk analysis the predictor variables were risk (continuous) and habitat type
204 (categorical) whereas for the immediate risk analysis the predictor variables were distance to nearest lion
205 and spotted hyaena (continuous) and habitat type (categorical). In each model the identity of the cheetah
206 was entered as a random factor. For both the long- and short-term risk, four *a-priori* candidate models
207 predicting the probability of cheetah presence as a function of risk and habitat type were created (Tables
208 2 and 3). Models were ranked using Akaike Information Criterion corrected for small sample size (AICc). If
209 one model was clearly dominant ($w_i > 0.9$) this was used, otherwise model averaging was performed to
210 estimate the parameters (Burnham & Anderson 2002). Statistical analyses were performed using
211 statistical software R 2.14.2 (R Development Core Team 2012).

212 **Results**

213 *Habitat selection*

214 Cheetahs showed significant habitat preferences both within the study area (2^{nd} order selection: λ =
215 0.068, p = 0.003) and within their home-ranges (3^{rd} order selection: λ = 0.035, p < 0.001). The home-
216 ranges of cheetahs included more grassland and mixed woodland than would be expected based on
217 overall availability within the study area, while the amount of mopane, riparian and swamp was lower.
218 Within their home-ranges, cheetahs preferred grassland over mixed woodland (Fig. 1). Similarly, lions

showed significant habitat preferences both within the study area (2nd order selection: $\lambda = 0.053$, $p < 0.001$) and within their home-ranges (3rd order selection $\lambda = 0.168$, $p = 0.014$). Lion home-ranges included more grassland and mixed woodland and less mopane and swamp than expected. However, within their home-ranges lions preferred mixed woodland over grassland (Fig. 1). Within the study area, spotted hyaenas preferred grassland and mixed woodland and avoided swamp (2nd order selection: $\lambda = 0.058$, $p = 0.002$; Fig. 1). Within their home-ranges, however, habitat selection was random; i.e. they used habitat types in proportion to their availability (3rd order selection: $\lambda = 0.120$, $p = 0.228$).

Influence of long- and short-term risk of encountering larger carnivores on the spatial distribution of cheetahs

The best models predicting the spatial distribution of cheetahs included habitat types, risk (both short- or long-term) and an interaction between these two predictor variables, suggesting that the effect of risk was dependent on habitat type (Tables 2 and 3).

Surprisingly, cheetahs were more likely to be found in areas where there was a high, long-term risk of encountering lions (Fig. 2 – top row). In other words, cheetahs did not actively avoid areas that were intensively used by lions. This was significant for all habitat types (grassland: $Z = 4.46$, $p \leq 0.001$, mixed woodland: $Z = 8.17$, $p \leq 0.001$, mopane: $Z = 8.34$, $p \leq 0.001$ and riparian: $Z = 2.89$, $p = 0.004$) apart from swamp ($Z = 0.30$, $p = 0.762$). The probability of finding a cheetah with regards to the long-term risk of encountering spotted hyaena was only significant for mixed woodland ($Z = -3.16$, $p = 0.002$) and mopane ($Z = 3.10$, $p = 0.002$). Cheetahs were less likely to be found in areas where there was a higher chance of encountering spotted hyaenas when they were in mixed woodland but were found in high risk areas in mopane (Fig. 2 – bottom row).

The probability of cheetah presence in relation to distance to the nearest lion varied depending on habitat type. In grassland and mopane, cheetahs were significantly further from lions than expected (grassland: $Z = 6.73$, $p \leq 0.001$; mopane: $Z = 4.05$, p $p \leq 0.001$) but in mixed woodland cheetahs were significantly closer to lions than expected ($Z = -3.99$, p $p \leq 0.001$; Fig. 3) indicating that habitat type possibly plays a role in the way that cheetahs perceive and respond to risk. Averaged over all habitat types, cheetahs were 5.10 ± 0.09 km (mean ± 95% CI) from the nearest collared lion. To the contrary, the distance to the nearest collared spotted hyaena did not significantly influence the probability of cheetah presence in any habitat type apart from swamp.

Discussion

Our results show that the response of cheetahs to the risks posed by the larger and competitively stronger lions and spotted hyaenas is predator-specific, habitat-specific and dependent on the immediacy of the risk. More specifically, we show that cheetahs' response to risk is reactive rather than predictive. In other words, cheetahs did not consistently avoid habitats and areas with a high likelihood of encountering lions or spotted hyenas (predictive response) but instead, adjusted their behaviour to short-term presence of lion risk (reactive response).

Whilst it has been suggested that less dominant species can minimise negative encounters with competitors or predators by selecting areas or habitat types that attract fewer predators and competitors, such as prey-poor areas (Chesson 1986; Rosenzweig 1991; Durant 1998), we did not detect any spatial segregation between cheetahs and lions or between cheetahs and spotted hyaenas both in terms of habitat use and long-term predation risk. The lack of predictive avoidance may result from 1) the fact that cheetahs do not directly benefit from avoiding areas of long-term predation risk, 2) the inability of cheetahs to detect and infer long-term risks, or 3) our failure to detect avoidance due to unaccountability of uncollared individuals. Whilst the latter may apply for spotted hyaenas (see below), we believe that this is not the case for lions since a significant proportion of the population was collared

(for more details see the Methods section). We also believe that if it was evolutionary advantageous to discriminate between risky and non-risky areas; cheetahs would have developed the ability to do so. It thus appears that cheetahs do not necessarily benefit from avoiding areas with a high chance of finding lions, results that are corroborated by recent findings in the Serengeti where Swanson et al. (in review) have shown that cheetahs do not avoid areas characterised by a high likelihood of encountering lions. As in the Serengeti, the extensive overlap in space and habitat use between cheetahs and lions is likely driven by the distribution and acquisition of similar resources such as prey. In our study, cheetahs and lions selected for grassland and mixed woodland both for the 2nd and 3rd order selection and avoided mopane. In the Okavango delta, impala, which represents 75 % of the diet of cheetahs (n=92) and 17 % of the diet of lions (n=118, F. Broekhuis unpublished data), prefer mixed woodland over mopane (van Bommel *et al.* 2006). The observed differences in habitat use between lions and cheetahs on a finer spatial scale can be attributed to differences in behavioural traits, such as hunting strategies, rather than active avoidance. For instance, being high speed hunters, cheetahs prefer more open habitats, while lions, being ambush hunters, are more successful in vegetated areas (Mills, Broomhall & du Toit 2004; Hopcraft, Sinclair & Packer 2005).

The immediate risk of encountering lions, however, appeared to be an important factor influencing the spatial distribution of cheetahs as the latter were generally further away from lions than would be expected under a random distribution. This suggests that lions pose a threat to cheetahs and that cheetahs can detect lion presence, assess the level of risk and adjust their behaviour accordingly, probably responding to more immediately and spatially reliable cues such as visual or auditory detection (Durant 2000; Webster, McNutt & McComb 2010). Interestingly, in mixed woodland cheetahs were found to be closer to lions than expected. Since it is unlikely that cheetahs would actively move towards lions, this suggests that when cheetahs are in denser vegetated habitats they either cannot detect lions or do not feel the need to avoid them. Either way, denser habitats, such as mixed woodland, may be a relatively

safe refuge for cheetahs as the reduced visibility is likely to reduce detection (Janssen et al. 2007), decreasing the likelihood of encounters with lions. This interpretation is supported by previous studies, which showed that vegetation cover minimised cheetah interactions with lions and spotted hyaenas (Bissett & Bernard 2007; Hunter, Durant & Caro 2007a). Similarly, elk have been shown to move into denser vegetation when wolves were nearby (Creel et al. 2005). Despite the fact that we believe there to be very little seasonal variation in the distribution and ranging behaviours of these carnivores we acknowledge that the six month windows used in this study are a relatively short time span. We therefore encourage longer studies to be carried out in the future to account for seasonality and stochasticity among years.

In general, cheetah response to both the long- and short-term risk was less pronounced for spotted hyaenas than for lions. Spotted hyaenas pose less of a threat to cheetahs and are less predictable than lions, mostly because spotted hyaenas are extremely flexible in their prey preference, foraging strategies and habitat selection (Kruuk 1972; Hayward 2006). Our results are thus consistent with past studies, which showed that cheetahs exhibited a less marked response to spotted hyaenas than to lions (Laurenson 1995; Durant 1998; Webster, McNutt & McComb 2010). It is, however, important to note that quantifying spotted hyaena risk was difficult due to their social system and structure. Spotted hyaenas live in large, hierarchical, fission-fusion social groups but, unless on a large carcass, they generally occur alone or in smaller sub-groups (Kruuk 1972, F. Broekhuis pers. obs.). By collaring several individuals in a clan, however, we feel that we had a good representation of their general space and habitat use. Nonetheless, the relatively large number of uncollared individuals may have influenced our results on short-term cheetah avoidance behaviour of spotted hyaenas.

Overall, risk avoidance is a reactive, rather than a predictive process - findings that are corroborate by other studies. For example, Creel et al. (2008) showed that elk did not increase their level of vigilance in areas where there was a higher risk of predation; vigilance levels were, however, higher when wolves

were in the immediate vicinity compared to when they were absent. Lima & Bednekoff (1999) suggested that previous experiences of variation in the risk (i.e. long-term risk) should influence an animals' behaviour in terms of the temporal, short-term, variation in risk. According to this risk allocation hypothesis (see also some empirical tests of this hypothesis; e.g. Sih & McCarthy 2002), as the overall time spent under risk increases, animals should increase their allocation of risky activities, such as foraging, during periods of high risk. Our findings could be interpreted in this framework; indeed, encounters of subordinate carnivores with larger carnivores are not uncommon in the study ecosystem and consequently would result in very costly loss of feeding opportunities if subordinate species would totally avoid larger carnivores. Our results thus highlight the importance of reactive responses in ecosystems where risks are widespread and recurrent.

In conclusion, we show that spatial resolution, temporal context and environmental complexity need to be taken into consideration to understand the mechanisms by which competing carnivores coexist. Whilst our results suggest that short-term space and habitat use is a hierarchical process firstly driven by resource acquisition and thereafter fine-tuned by predator avoidance (also see Cozzi *et al.* 2012) we encourage a more dynamic approach to investigate interactions between species.

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Figures

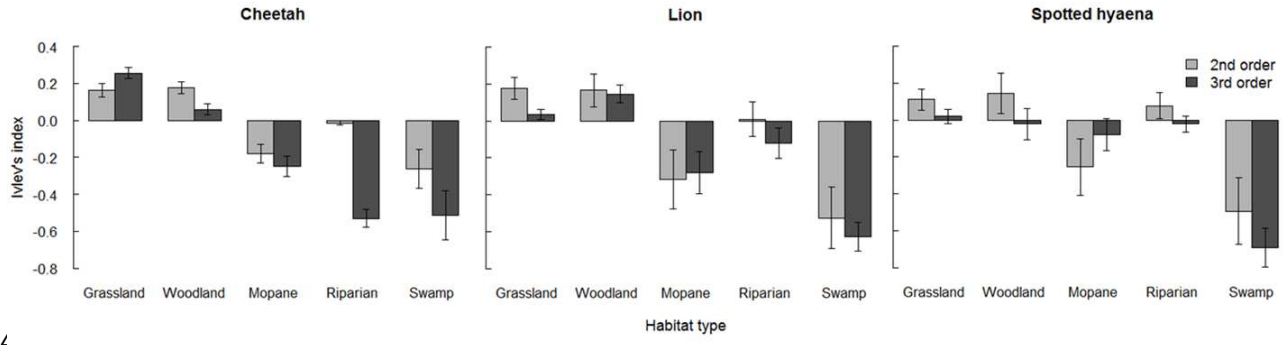
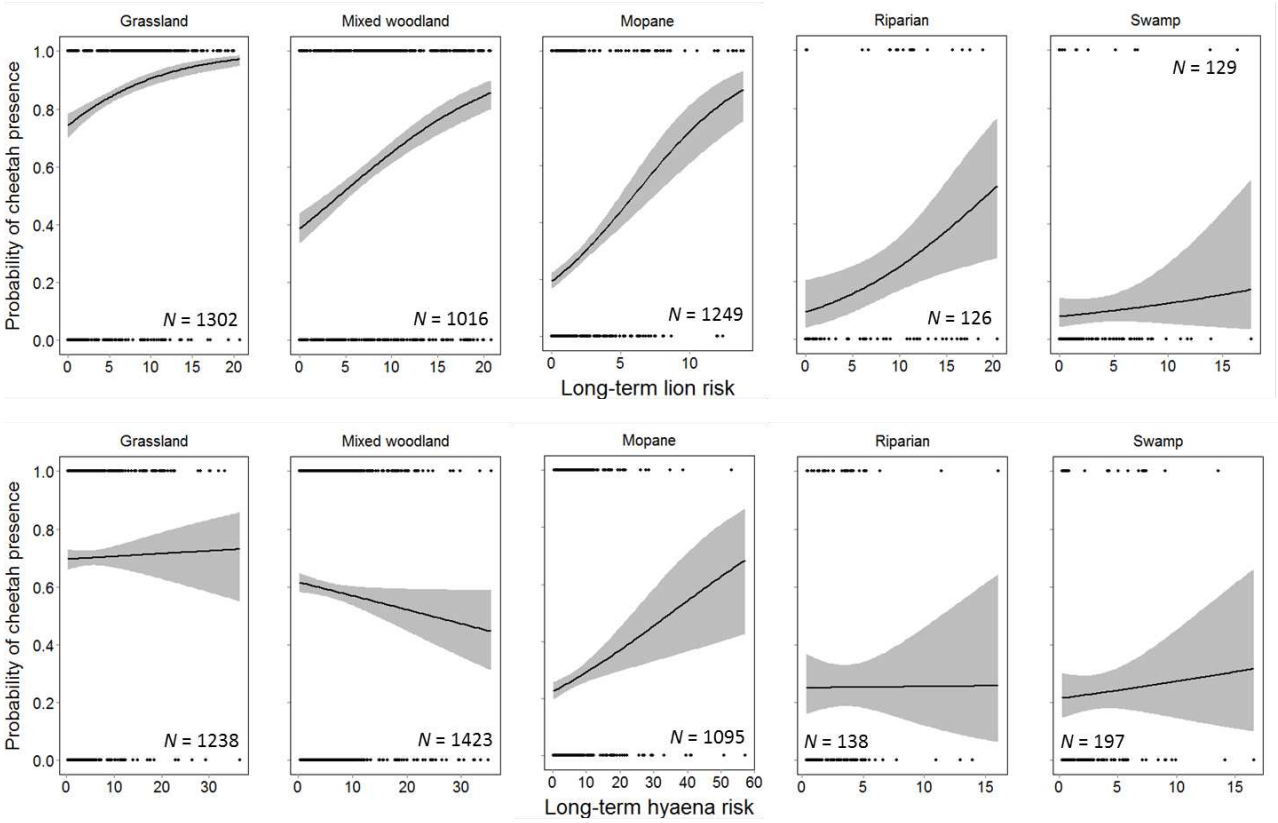


Fig. 1: Habitat selection for cheetahs (n=6), lions (n=5) and spotted hyaenas (n=8) in northern Botswana using the Ivlev's index for preference/avoidance. Values >0 indicate that a habitat type was used more than available (preference) and values <0 indicate habitat types that were used less than available (avoidance). The analysis was carried out on two levels; 2nd order (light grey – home-ranges vs. study area) and 3rd order (dark grey – locations vs. home-ranges) habitat selection (Johnson 1980).



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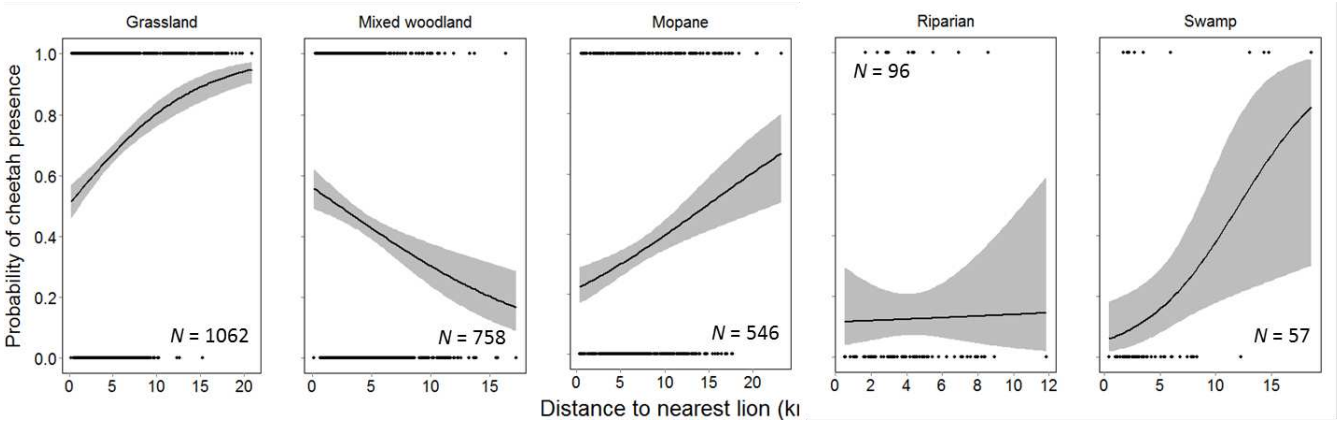
471 **Fig. 2:** Relationship between the long-term encounter risk of encountering lions (top row) and spotted
472 hyaenas (bottom row) and the probability of cheetah presence in different habitat types. Long-term risk is
473 proportional to the likelihood of predator presence calculated using kernel density estimates (KDE) at a 50 x
474 50m resolution. Fitted lines are displayed ± 95% confidence intervals.



475

476 **Fig. 3:** Relationship between the immediate risk of encountering lions, determined by the distance to the
477 nearest lion, and the probability of cheetah presence in different habitat types. Fitted lines are displayed ± 95%
478 confidence intervals.

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Figure legends

Fig. 1: Habitat selection for cheetahs (n=6), lions (n=5) and spotted hyaenas (n=8) in northern Botswana using the Ivlev's index for preference/avoidance. Values >0 indicate that a habitat type was used more than available (preference) and values <0 indicate habitat types that were used less than available (avoidance). The analysis was carried out on two levels; 2nd order (light grey – home-ranges vs. study area) and 3rd order (dark grey – locations vs. home-ranges) habitat selection (Johnson 1980).

Fig. 2: Relationship between the long-term encounter risk of encountering lions (top row) and spotted hyaenas (bottom row) and the probability of cheetah presence in different habitat types. Long-term risk is proportional to the likelihood of predator presence calculated using kernel density estimates (KDE) at a 50 x 50m resolution. Fitted lines are displayed ± 95% confidence intervals.

Fig. 3: Relationship between the immediate risk of encountering lions, determined by the distance to the nearest lion, and the probability of cheetah presence in different habitat types. Fitted lines are displayed ± 95% confidence intervals.

Tables

Table 1: Summary of the five main habitat types found in the Okavango Delta, Botswana. Habitat classification was based on vegetation composition (type of vegetation) and structure (open-medium-dense).

Habitat type	Vegetation composition	Vegetation structure	Area (km^2)*	%*
Grassland	Former floodplains characterised by shrubbed grassland dominated by *Cynodon dactylon*, *Chloris virgata* and *Eragrostis spp*.	Open	411	15.1
Mixed woodland	Predominately *Acacia spp.* with a grassy understory consisting of *C. dactylon*, *Panicum spp.* and *Eragrostis spp.*	Medium	638	23.5
Mopane	Characterised by *C. mopane* shrubs and trees	Medium/ dense	1201	44.1
Riparian	Tall mixed woodland located on (historic) riverine areas characterised by *A. nigrescens* and *Combretum imberbe* trees	Dense	143	5.3
Swamp	Moist and seasonally flooded open grasslands usually along a river course characterised by sedges and grass species *Panicum repens* and *C. dactlyon*	Open	326	11.9

*Area and percentage of the core study area. The core study area was defined by the outermost boundary delimiting the total sum of the 90% kernels of all three species (cheetahs, lions and spotted hyaenas).

Table 2: Summary of model selection statistics for the Generalised Linear Mixed Models (GLMMs) analysing the probability of cheetah occurrence (presence/absence) in relation to habitat type and long-term predator risk (six months). Models were ranked according to Akaike weights (w_j) based on the Akaike Information Criterion for small samples (AICc). Included are the number of parameters (K), the log likelihood and the AICc differences (Δ_i).

Predator	**Rank**	**Model**	**K**	**log likelihood**	**AICc**	**Δ_i**	**w_i**
Lion	1	habitat type x risk	11	-1811.56	3645.20	0	1.00
	2	habitat type + risk	7	-1829.65	3673.34	28.14	0.00
	3	habitat type	6	-1903.70	3819.43	174.22	0.00
	4	risk	3	-2188.44	4382.89	737.69	0.00
Spotted hyaena	1	habitat type x risk	11	-2530.50	5083.07	0.00	0.99
	2	habitat type	6	-2540.29	5092.60	9.53	0.01
	3	habitat type + risk	7	-2540.21	5094.45	11.38	0.00
	4	risk	3	-2832.18	5670.37	587.30	0.00

508 **Table 3:** Summary of model selection statistics for the Generalised Linear Mixed Models
509 (GLMMs) analysing the probability of cheetah occurrence (presence/absence) in relation to
510 habitat type and the immediate predator risk measured as the distance to nearest predator.
511 Models were ranked according to Akaike weights (w_j) based on the Akaike Information Criterion
512 for small samples (AICc). Included are the number of parameters (K), the log likelihood and the
513 AICc differences (Δ_i).

Predator	Rank	Model	K	log likelihood	AICc	Δ_i	w_i
Lion	1	habitat type x distance	11	-1554.19	3130.48	0	1.00
	2	habitat type + distance	7	-1586.17	3186.38	55.90	0.00
	3	habitat type	6	-1603.39	3218.82	88.34	0.00
	4	distance	3	-1732.89	3471.79	341.31	0.00
Spotted hyaena	1	habitat type x distance	11	-2736.42	5494.89	0.00	0.63
	2	habitat type	6	-2742.38	5496.77	1.88	0.25
	3	habitat type + distance	7	-2742.12	5498.27	3.37	0.12
	4	distance	3	-2895.27	5796.55	301.66	0.00

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